SHORTER ARTICLES AND DISCUSSION

ON THE INHERITANCE OF TRICOLOR COAT IN GUINEA-PIGS, AND ITS RELATION TO GALTON'S LAW OF ANCESTRAL HEREDITY[1]

In 1889 the late Francis Galton formulated a "law of ancestral heredity" which he believed would prove to be of general applicability in as much as he had already applied it with gratifying results to two widely different categories of cases, viz., the height of man and the color of dogs. The law as stated by Galton is:

> The two parents contribute between them, on the average one-half, or (0.5) of the total heritage of the offspring; the four grandparents, one-quarter, or $(0.5)^2$; the eight great-grandparents, one-eighth, or $(0.5)^3$, and so on.

The validity of Galton's law has since been seriously called in question, though neither of his two cases has yet received a wholly satisfactory explanation, but sufficient progress has been made in the study of heredity to show the unsoundness of the basic principle on which Galton's generalization rested. In reality there is no such thing as "*ancestral*" inheritance; for we inherit from our parents only, not from our more remote ancestors. It is true that a knowledge of the more remote ancestry may help us to understand better what we have inherited from our parents, but it is clear that such knowledge of the ancestors will not enable us to predict the character of their descendants in the precise manner outlined by Galton. In a specific case, the inheritance of albinism in mice, I made in 1903 a test of the comparative value of Galton's law and Mendel's law in predicting the character of offspring, with the result that Mendel's law gave predictions closely according with observation, whereas predictions based on Galton's law proved wholly unreliable.

As regards height, however, and other size characters, Galton's law is quite as good a basis for predicting the result of particular matings as is Mendel's. Indeed it is not clear that either of them is applicable to such cases as human stature.

[1] From the Laboratory of Genetics of the Bussey Institution, Harvard University.

The other case studied by Galton, the inheritance of the tricolor condition in Bassett hounds, no one up to the present time has attempted to explain on any ground other than that taken by Galton in his law of ancestral heredity, although it is now generally conceded that his law does not apply to color inheritance in general.

The tricolor condition seen in dogs is found in very few other animals, one of which however is the guinea-pig, the tricolor variety of which I have had an opportunity to study for some years. The observations made on tricolor guinea-pigs throw light on the facts observed by Galton regarding tricolor dogs. They show wherein Galton's interpretation fails and what advantages a Mendelian interpretation has as applied to this case.

The tricolor condition of guinea-pigs is one of long standing. Cuvier reports it as depicted by Aldrovandus, who made the first scientific description of the guinea-pig, soon after 1550. This color variety had probably been in existence for a long time before the discovery of America. The natives of Peru still rear it for food in the recesses of their adobe cabins, as their ancestors have doubtless done for untold centuries. Nevertheless it does not breed true, and can not be made to do so.

The tricolor animal is white marked with irregular but distinct blotches of black and yellow. Tricolors produce besides tricolors young which are black-and-white or yellow-and-white, but never in my experience those which are wholly free from white. In other words they breed true to spotting with white, but not to spotting with black and yellow. The black-and-white as well as the yellow-and-white offspring of tricolor parents may produce tricolor young. Indeed any one of these three conditions is able to produce both the others. See Table. Nothwithstanding the

TABLE SHOWING THE KINDS OF YOUNG PRODUCED BY A RACE OF GUINEA-PIGS CONTAINING TRICOLOR INDIVIDUALS

B-W, black-and-white; *Y-W*, yellow-and-white; *T*, tricolor

Parents	Young			
	T	*B-W*	*Y-W*	Per Cent. *T*
T × *T*...	8	1	5	57
T × *B-W*...	9	3	5	53
T × *Y-W*...	13	2	9	54
B-W × *B-W*...	1	3	2	17
B-W × *Y-W*...	6	1	1	75
Y-W × *Y-W*...	9	2	9	45
Totals...	46	12	31	52

fact that neither the black-and-whites nor the yellow-and-whites produced by tricolors breed true, there are races of black-and-white and of yellow-and-white guinea-pigs which do breed true. It remains to explain why the others do not. A black-and-white animal which breeds true may be considered to possess some chemical substance necessary for the production of color (which we call a color-factor) distributed irregularly throughout its coat. Wherever this substance is wanting no color is formed and a white area results. The specific factor for black (probably an enzyme) is however everywhere present in the coat so that wherever color forms the color is black. Such races as this breed true.

The yellow-and-white animal which breeds true may likewise be considered to have an irregularly distributed color-factor, but to lack entirely in its coat the black factor. Hence the color, wherever formed, is yellow.

Yellow races also exist which do not bear spots of white, but which have spots of black. In such animals the color-factor is evidently uniform in distribution, whereas the black factor is irregularly distributed.

Now the tricolor race is a yellow one spotted both with white and with black, *i. e.*, it results from irregularity in distribution through the coat of two different chemical substances, the color factor and the black factor. These two factors are known to be independent of each other in heredity. See Castle (1909). It is therefore not to be supposed that they will commonly coincide in distribution. If the black factor extends over all the colored areas, the animal will be black-and-white. If the black factor falls only on areas which lack the color factor, it will produce no visible effect, and the animal will be yellow-and-white. If, finally, the black factor falls on some of the colored areas but not on all of them, those in which it falls will be black, the others yellow, and the uncolored areas of course white. Hence a tricolor will result. But the gametic composition of these tricolors will not be different from that of the black-and-whites or red-and-whites produced by the same race, since all alike will be characterized by irregularity in distribution of the same two factors. A tricolor race on this hypothesis should be unfixable, as has up to the present time been found to be true.

The same line of explanation will answer equally well for the case of the Bassett hounds studied by Galton. These Galton

classifies as either "tricolor" or "non-tricolor" ("lemon-and-white"). A third variety, "black-and-tan," is mentioned by Galton, but disregarded in his statistical treatment. He does not state whether it may or may not possess white spots, but I strongly suspect that the "black-and-tans" produced by spotted Bassett hounds would also be spotted, in which case they would correspond with the category black-and-white of guinea-pig races containing tricolors. For the "tan" feature of black-and-tan dogs is in reality due to a pattern factor as distinct from black as is the agouti pattern of guinea-pigs. Hence so far as spotting is concerned Galton's disregarded "black-and-tans" were probably black-and-whites which happened to possess the "tan" pattern (light spot over eye, light belly and legs below). If so, the behavior of the dogs accords in every point with that of the guinea-pigs as regards color inheritance. For Galton observed that neither tricolors nor non-tricolors breed true, but each sort may produce the other, though it produces *more* of its own kind. The same is true for guinea-pigs; see Table. It is desirable that any one having the opportunity should look into the breeding capacity of Bassett hounds which are black-and-white or "black-and-tan." If they can produce "tricolor" and "lemon-and-white young," the parallel between the breeding capacity of tricolor guinea-pigs and tricolor dogs will be completely established.

W. E. CASTLE

BUSSEY INSTITUTION,
HARVARD UNIVERSITY

BIBLIOGRAPHY

Castle, W. E.
1903. The Laws of Heredity of Galton and Mendel, and Some Laws Governing Race Improvement by Selection. *Proc. Amer. Acad. of Arts and Sci.*, Vol. 39, pp. 223–242.
1905. Heredity of Coat Characters in Guinea-pigs and Rabbits. Carnegie Institution of Washington, Publication No. 23.

Castle, W. E., in collaboration with H. E. Walter, R. C. Mullenix and S. Cobb.
1909. Studies of Inheritance in Rabbits. Carnegie Institution of Washington, Publication No. 114.

Cumberland, C.
1901. The Guinea-pig or Domestic Cavy. 100 pp. illustr. London, L. Upcott Gill.

Galton, F.
1889. Natural Inheritance. Macmillan Co., London and New York.
1897. The Average Contribution of Each Several Ancestor to the Total Heritage of the Offspring. *Proc. Roy. Soc. London*, Vol. 61, pp. 401–413.